

Patch edges and insect populations

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Abstract Responses of insect populations may be related to patch size and patch edge responses, but it is not clear how to identify these rapidly. We used a random-walk model to identify three qualitative responses to edges: no edge effect (the null model), reflecting edges and absorbing edges. Interestingly, no edge effect meant that abundance was lower at edges than in the center of patches, and reflecting edges have similar abundance at edges and centers. We then characterized several insect species' response within maize plots to patch edges and patch size, using a simple, quick, qualitative experiment. *Coleomegilla maculata* and *Trichogramma* spp. were the only organisms that responded to patch size and edges as patch theory and the null edge model would predict. *Ostrinia nubilalis* larvae and possibly *Rhopalosiphum maidis* and eggs of *Chrysopa* spp. responded to patch size and edges as predicted by an attracting edge model. Estimation of predation rates suggested that the spatial distribution of these species might be determined by predators. Edge effects or the lack thereof relative to patch size may be rapidly determined for arthropod species, which could lead to understanding the mechanism(s) underlying these effects. This information may be useful in reaction diffusion models through a

scaling-up approach to predict population structure of species among patches in a landscape.

Keywords Agroecosystems · Boundaries · Edge effects · Patchiness

Introduction

There has been a long-standing interest in species responses to habitat edges, but with a few exceptions (Cantrell and Cossner 1993; Fagan et al. 1999, Ries and Sisk 2004), most studies to date have been largely descriptive. Cantrell and Cossner (1993) and Fagan et al. (1999) introduced spatially explicit quantitative models for understanding edge effects. In the model developed by Cantrell and Cossner (1993) for species that are found more often at the edges of patches, boundary conditions are stipulated along the exterior boundary of the ecotone (outside of edge) and along the interior boundary (inside of edge) of the ecotone “internal interface”. In contrast, in the model developed by Fagan et al. (1999) for species that are restricted to a single kind of patch, edges are considered to be thin, and the area surrounding a patch is assumed to be immediately lethal. Ries and Sisk (2004) developed a conceptual model based on a species' resource distribution that predicts whether an organism's abundance near edges is expected to increase, decrease or remain the same based on the distribution of resources of the species. They modeled two adjoining patches and predicted species abundance based on the relative quality of the resources within each patch and found that their model could predict abundances of many bird and butterfly species that have been reported in published studies. However, for many insect species, it is difficult to obtain a priori knowledge of their often

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competing and diverse resource needs (e.g. food and hosts for parasitoid species, mates and shelter), which is further confounded by their potentially rapid temporal change and fine-scale spatial variability. In addition, although an increasing number of studies indicate that factors at the landscape scale, such as landscape complexity, land-use intensity and vegetative connectivity, shape insect populations at the local or field scale (Roschewitz et al. 2005; Schmidt et al. 2005; Schweiger et al. 2005), many arable landscapes lack variability in these factors (e.g. highly cultivated land in much of the United States). Thus, in many cases, it may be easier to determine if edge effects are present in a given patch for a species and then to investigate the underlying mechanism(s) in order to understand and predict species responses among patches.

In addition, because many insect species respond to patch size as well as patch edges (e.g. Kareiva 1983, 1985; Marino and Landis 1996; Blackshaw and Arcy-Burt 1997; Svensson et al. 2000; Magura 2002), it may be useful to consider the interaction of these factors on the distribution of populations among patches within a landscape. The theory of patch size has concentrated on determining the critical size below which a population will not be able to sustain itself (Slobodkin 1961; Okubo 1984). The focus of this theory is on the balance between the net movement of organisms out of the patch and the reproduction of organisms in the patch. If net movement is proportional to the length of the perimeter of the patch and reproduction is proportional to the area of the patch, then population growth will be related to the perimeter-to-area ratio of a patch. Small patches with high perimeter-to-area ratios will have low population growth, and large patches with low perimeter-to-area ratios will have high population growth. Thus, a corollary is that population density will be higher in larger patches. This theory assumes, however, that the characteristics of patch edges are the same as those in the center of the patch, and for some insect species this may not be true (Dyer and Landis 1997; Winder et al. 1999; Braschler and Baur 2003). Insect population dynamics within and among patches will be greatly complicated by edge effects because the number of interaction effects among edges and patch centers in a landscape will be roughly the square of the number of effects if edge effects were absent.

In this paper, we emphasize simple, qualitative empirical tests of theoretical predictions to determine if more complex edge models are necessary to understand population dynamics in landscapes. We do not attempt to parameterize theoretical models quantitatively with field data, but rather focus on a rapid, qualitative assessment of the existence of edge effects relative to patch size. We start by providing simple theoretical predictions for a null-edge model to facilitate rapid detection of edge effects from field

data. We then conduct some simple field experiments to evaluate how some insect species respond to patch size and edges and discuss how more complex models can be used to predict population dynamics of these species in larger landscapes.

Qualitative theoretical predictions for null-edges

We simulated edge effects on theoretical patches to develop a null-edge hypothesis and to illustrate how insect population density could respond qualitatively to patch edges. A null-edge hypothesis is the predicted population response to edges when there is no differential mortality or reproduction between patch edges and patch centers. Using a random walk of individuals, we modeled patches and edge effects by the variation in birth/death rates and movement.

The dynamical processes at each site subjected individuals to mortality, to redistribution to neighboring sites and, finally, to reproduction according to specified probabilities. The expected number of individuals at site x at time $t + 1$ is

$$E[N(x, t + 1)] = B_x(1 - m_x)s_xN(x, t) + d_{x-1,x}m_{x-1}s_{x-1}N(x - 1, t) + d_{x+1,x}m_{x+1}s_{x+1}N(x + 1, t),$$

where $E[N(x, t + 1)]$ is the expected number of individuals at $(x, t + 1)$, B_x is the expected per capita reproduction rate at site x , given survival and movement; m_x is the conditional probability of movement from site x , given survival; s_x is the probability of survival at site x ; d_{ij} is the conditional probability of moving from site i to site j , given that the individual survives and departs from site i ; and $N(x, t)$, $N(x - 1, t)$ and $N(x + 1, t)$ are the number of individuals at (x, t) , $(x - 1, t)$, and $(x + 1, t)$ respectively. $B_x = 1 + b_x$, where b_x is the conditional probability of reproduction, given movement and survival. This model is essentially a discrete version of Fagan et al.'s (1999) model.

We considered three kinds of edges. In the null model, the edges have similar probabilities of insect survival, movement, direction of movement, reproduction and survival as the center of the patch. In the second model, the edges reflect individuals back into the patch, which means that the direction of movement is modified at edges, but the probabilities of survival, movement within the patch and reproduction are the same as the center of the patch. In the third model, the edges attract individuals that move into the edge, or the probability of movement from an edge site is less than from a central site, but the probabilities of survival, direction of movement and reproduction are the same as the center of the patch. This attracting edge model is different than that of Fagan et al.'s (1999) absorbing

edge model in that organisms are not lost to the patch but are differentially distributed within the patch, and it is similar to a biologically attractive edge. In addition, the attracting edge model differs from Fagan et al. (1999) by assuming that the environment outside of the patch is merely unsuitable for reproduction. In all other respects, the environment outside the patch is the same as inside the patch and implies that individuals that leave the patch may return to the patch.

These conditions were simulated on 20-site linear patches using Monte Carlo techniques (Fig. 1). Twenty simulations for each set of parameters were run for 30, 40 and 50 time steps. The specific parameter values are shown in Appendix S1 in the [Electronic Supplementary Material \(ESM\)](#). All sites started with five individuals.

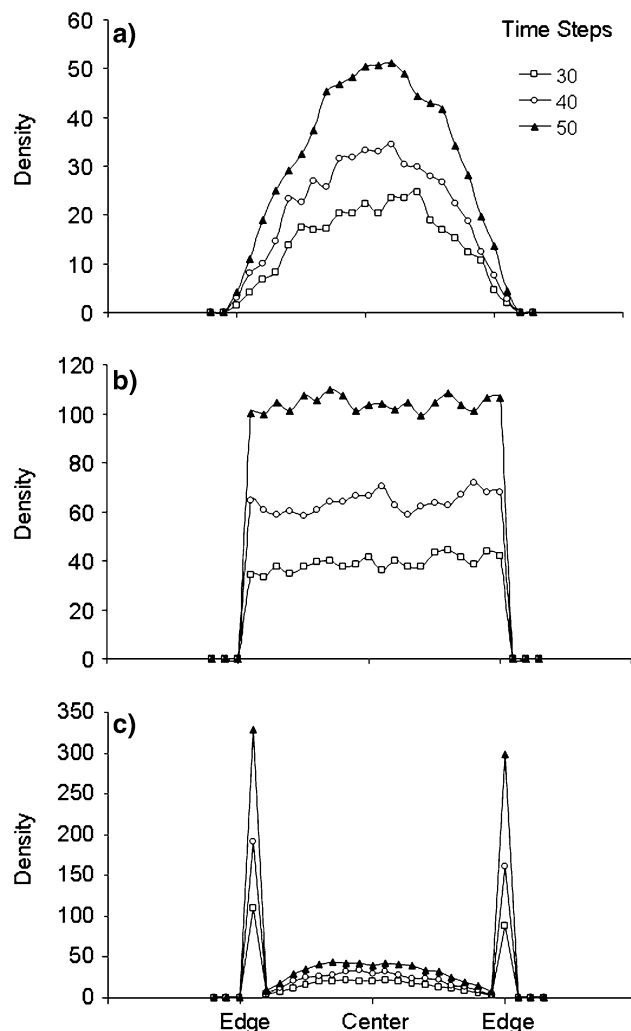


Fig. 1 Simulated insect densities on patches: **a** null model, **b** reflecting edges, **c** attracting edges. These conditions were simulated on 20-site linear patches using Monte Carlo techniques. Twenty simulations for each set of parameters were run for 30, 40 and 50 time steps. All sites started with five individuals

For the null model, population density at patch edges was lower than in the center of the patch (Fig. 1a). Conversely, the density outside the patch was higher near the patch than farther away from the patch. When a patch with a good reproductive environment adjoined a patch with a poor reproductive environment, and survival and movement was uniform in both environments, then density at the edges of the good reproductive environment was lower and the density at edges of the poor reproductive environment was higher compared with the density in the center of each respective environment. Thus, the null-edge hypothesis is that populations will be at lower densities at patch edges when adjacent to a poorer patch and at higher densities in poorer patches when adjacent to a better patch.

For completely reflecting edges, population density at patch edges was similar in the edge and center of patches (Fig. 1b). Reflecting edges equalized edge and center densities, but they did not elevate edge densities higher than center densities. Further directional movement toward edges within patches with reflecting edges would be necessary to elevate edge densities higher than center densities. For completely attracting edges, population density at patch edges was higher than in the center of the patch (Fig. 1c). Attracting edges elevated edge densities higher than center densities and also created a density trough near the edge. These edge effects are generated only from differences in movement behavior at edges versus the center of patches.

Edge effects result from several factors, including differential birth and survival, the relative quality of the adjoining patches in addition to the details of the movement behavior of organisms (e.g. Bach 1984; Kareiva 1987, for insects). Edge effects can influence the population density that is internal to the edge, as illustrated by the null model and the attracting-edge model. Insect population density can be higher or lower at edges depending on these factors, and as Fagan et al. (1999) have discussed – and as has been illustrated for insects and mites for strongly reflective edges (Kaiser 1983; Kareiva 1987; Kareiva and Perry 1989) – differential distribution at habitat edges affects species interactions and influences the composition and dynamics of ecological communities. In summary, when adjacent to a poorer patch, edge effects are occurring if edge densities are greater than or equal to densities in patch centers. If edge densities are lower than in patch centers, there may be no edge effect or, at least, no behavioral response to edges.

Material and methods

We used these predictions of the simple null-edge model to develop a simple and quick test for edge effects in a

prevalent and recurring insect community associated with maize in southeastern Minnesota, USA. The species sampled were *Rhopalosiphum maidis* (Fitch) [Hemiptera: Aphididae], eggs of *Chrysopa* spp. [Neuroptera: Chrysopidae], larvae of *Ostrinia nubilalis* (Hübner) [Lepidoptera: Crambidae], *Trichogramma* spp. [Hymenoptera: Trichogrammatidae] and adults and larvae of three coccinellid species, *Hippodamia tredecimpunctata* (Say), *Hippodamia convergens* (Guerin) and *Coleomegilla maculata* (DeGeer) [Coleoptera: Coccinellidae]. The corn leaf aphid, *R. maidis* is the dominant aphid in maize in the USA and forms large aggregations in the whorl. Adult *Chrysopa* spp. feed on nectar, honeydew and pollen, and larvae feed on aphids, mites, thrips, whiteflies and lepidopteran eggs and small larvae. European corn borer, *O. nubilalis* is a major pest of maize but also feeds on many other crops. *Trichogramma* spp. are minute egg parasitoids of primarily lepidopteran eggs. In Minnesota, *H. tredecimpunctata*, *H. convergens* and *C. maculata* are found in wetlands, meadows and small-grain and alfalfa fields in early spring and in maize fields from late spring until fall (Schellhorn and Andow 2005). Adults and larvae use aphids as their main food source but also feed on lepidopteran eggs and larvae, maize pollen, extrafloral nectaries and maize rust spores (Schellhorn and Andow 2005).

Irrigated maize (Pioneer 3906) was planted at the Sand Plains Research Station at Becker, Minnesota for two growing seasons using conventional practices. Three different-sized patches of maize were established: six small patches were 5.8×7.3 m, six medium-sized patches were 12.8×13.4 m and two large patches were 21.9×26.6 m. All patches were surrounded by at least 2.2 m of bare ground. The field was bordered by winter wheat to the north, dirt roads and hedge rows to the east and south and a hedgerow and bare ground fallow land to the east. At the time of sampling, the wheat field was senescing.

In both years, freshly laid egg masses of *O. nubilalis* were pinned to maize plants (Andow and Risch 1985): three times the first year and six times that second year. Egg masses were placed on three maize plants on each of the four edges and on 12 plants in the centers of each patch, exposed to natural enemies for 1 or 3 days, collected and reared in the laboratory. We analyzed the results separately for eggs exposed for 1 day and those exposed for 3 days. Percentage observed parasitism (P_o) was adjusted for predation (Andow 1990) to percentage expected parasitism (P_E) by $P_E = P_o / (100 - P_p)$, where P_p is percentage preyed upon.

In the second year, plant height, plant stage and counts of insects present were measured on three plants on each of the four edges and on 12 plants in the centers of each patch, as described above. On each plant sampled, we counted the number of adult and nymph *R. maidis*, of eggs of *Chrysopa*

spp., of larvae of *O. nubilalis*, and of adults, larvae and pupae of *H. tredecimpunctata*, *H. convergens* and *C. maculata*. We minimized disturbance to the insects by using hand mirrors to check the undersides of leaves. We pooled all coccinellid larvae and pupae because at the time of the study we could not accurately identify them to species. Plant height and stage were measured until the tassel stage.

Statistical analysis of the fate of egg masses of *O. nubilalis* was done with log-linear models for contingency tables, using year as a factor. Analysis of insect densities and plant height was performed with repeated measures ANOVA. Analysis of *O. nubilalis* larval density from dissections was done with ANOVA, with means separated with Tukey's HSD (SAS Institute 1998). In all cases, patches served as replicates, and edge/center was used as the first split plot. No transformation of *R. maidis* and *Chrysopa* spp. density improved the fit of the model; therefore, we report the analysis of the untransformed data.

Results

There was a significant date by patch size by position (edge/center) interaction on the density of *R. maidis* and adult *C. maculata*, and eggs of *Chrysopa* spp. ($F_{8,100} = 4.14$, $P < 0.0001$; $F_{8,100} = 7.76$, $P < 0.0001$; $F_{8,100} = 2.10$, $P = 0.042$, for *R. maidis*, *C. maculata* and eggs of *Chrysopa* spp., respectively). The density of *R. maidis* was significantly higher at the edges of the medium and large patches early in the year (Fig. 2b–c; $t = 5.30$, $df = 100$, $P < 0.001$ and $t = 7.79$, $df = 100$, $P < 0.001$ for medium and large plots on Julian date 184, respectively), but it was significantly higher in the center of the medium patches later in the year (Fig. 2b; $t = 2.27$, $df = 100$, $P = 0.025$ on = Julian date 223). The density of *Chrysopa* spp. eggs was significantly higher on July 21 (Julian date 202) at the edge of large patches than in the center of the patch (Fig. 2f; $t = 5.93$, $df = 100$, $P < 0.001$). The density of *C. maculata* was similar at the edge and the center of small patches over time, but their density was significantly higher in the center than the edges of medium and large patches on Julian date 223 (Fig. 2g–i; $t = 15.15$, $df = 100$, $P < 0.001$ and $t = 6.32$, $df = 100$, $P < 0.001$ for medium and large plots, respectively). There was no significant date-by-size-by-position interaction on the density of coccinellid larvae and pupae ($F_{8,100} = 0.05$, $P = 1.000$) or on adult *Hippodamia* spp. ($F_{8,100} = 0.26$, $P = 0.997$). There were no higher order interactions involving date on egg hatch, predation and disease so these interactions were removed from the model (Appendix S2 in [ESM](#)).

There was a significant interaction between patch size and position on the density of *R. maidis* ($F_{2,100} = 5.64$, $P = 0.005$) and adult *C. maculata* ($F_{2,100} = 4.59$, $P = 0.012$).

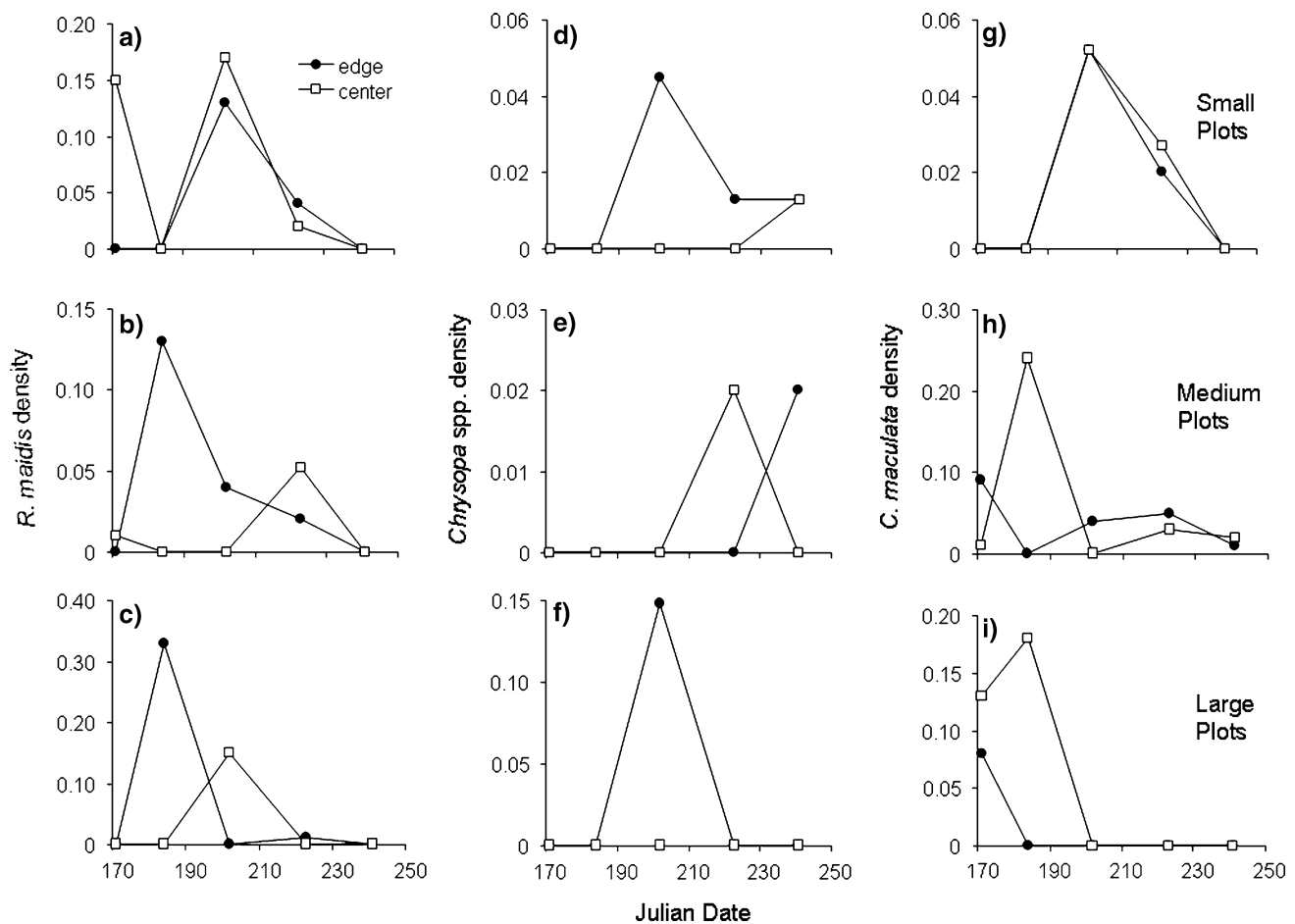


Fig. 2 Density of adult *Rhopalosiphum maidis* (a–c), *Chrysopa* spp. eggs (d–f) and adult *C. maculata* (g–i) in relation to date, patch size and location within the patch. $n = 72$

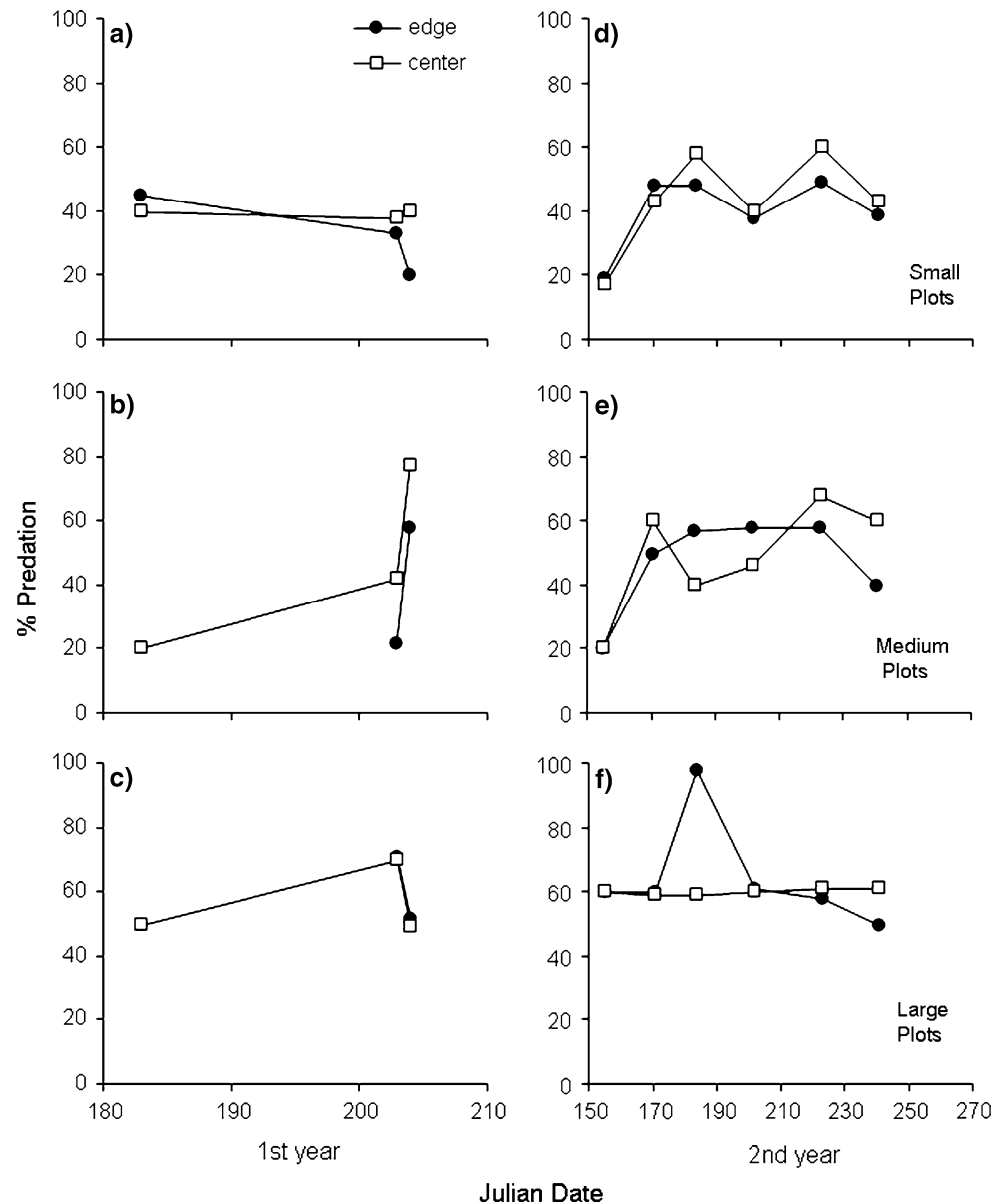
Significantly more *R. maidis* were found at field edges of medium and large patches (Fig. 2b, c), and significantly more *C. maculata* were found in the center than in the edges of medium and large patches, whereas small patches showed no effects of position on the density of either species (Fig. 2d–f). There were no patch size and position interactions on egg predation, hatch and disease (Appendix S2 in ESM; Figs. 3a–f, 4a–f, 5a–f).

There was a significant effect of patch size on *O. nubilalis* larvae and parasitism and predation rates of *O. nubilalis* eggs. Higher densities of *O. nubilalis* larvae ($F = 3.10_{2,599}$, $P = 0.046$), and higher rates of parasitism and predation occurred in larger patches (Appendices S2 and S3 in ESM; Fig. 3a–f). Egg hatch was significantly higher in small than medium and large patches (Fig. 4a–f), and disease symptoms of eggs were significantly less frequent in larger patches (Fig. 5a–f). Patch size had no significant influence on the density of *Chrysopa* spp. eggs ($F_{2,100} = 0.38$, $P = 0.687$), adult *Hippodamia* spp. (Table 1) and immature coccinellids ($F_{2,100} = 0.115$, $P = 0.320$).

There was also a significant species-specific response to patch edges. Significantly higher densities of both *O. nubilalis* larvae ($F_{1,599} = 200.53$, $P < 0.001$, $n = 300$) and rates of egg hatch and disease occurred at edges (ESM S2; Figs. 4a–f, 5a–f). Significantly lower rates of parasitism by *Trichogramma* spp. and rates of egg predation occurred at edges (Table 1; Appendix S2 in ESM; Fig. 3a–f). Adult *Hippodamia* spp. ($F_{1,10} = 0.01$, $P = 0.914$), *Chrysopa* spp. eggs ($F_{1,10} = 1.76$, $P = 0.214$) and immature coccinellids ($F_{1,10} = 0.02$, $P = 0.900$) had similar densities at edges as at the center of patches (Table 1; Fig. 2d–f). Adult *C. maculata* and *Hippodamia* spp. also tended to be more abundant on the north edges of the patches, the side closest to the wheat field ($F_{3,10} = 2.56$, $P = 0.054$ and $F_{3,10} = 2.52$, $P = 0.056$ for *C. maculata* and *Hippodamia* spp., respectively). No other species showed any directionality with respect the sides of the patch ($P > 0.05$).

There was a significant interaction between date, patch size and position on the height of maize plants ($F_{4,56} = 2.58$, $P = 0.047$). Maize plants were shorter early

Fig. 3 Percentage predation (a–f) of *Ostrinia nubilalis* egg masses in relation to date, patch size and location within the patch



in plant growth at edges, but attained similar heights as the center plants at the tassel stage.

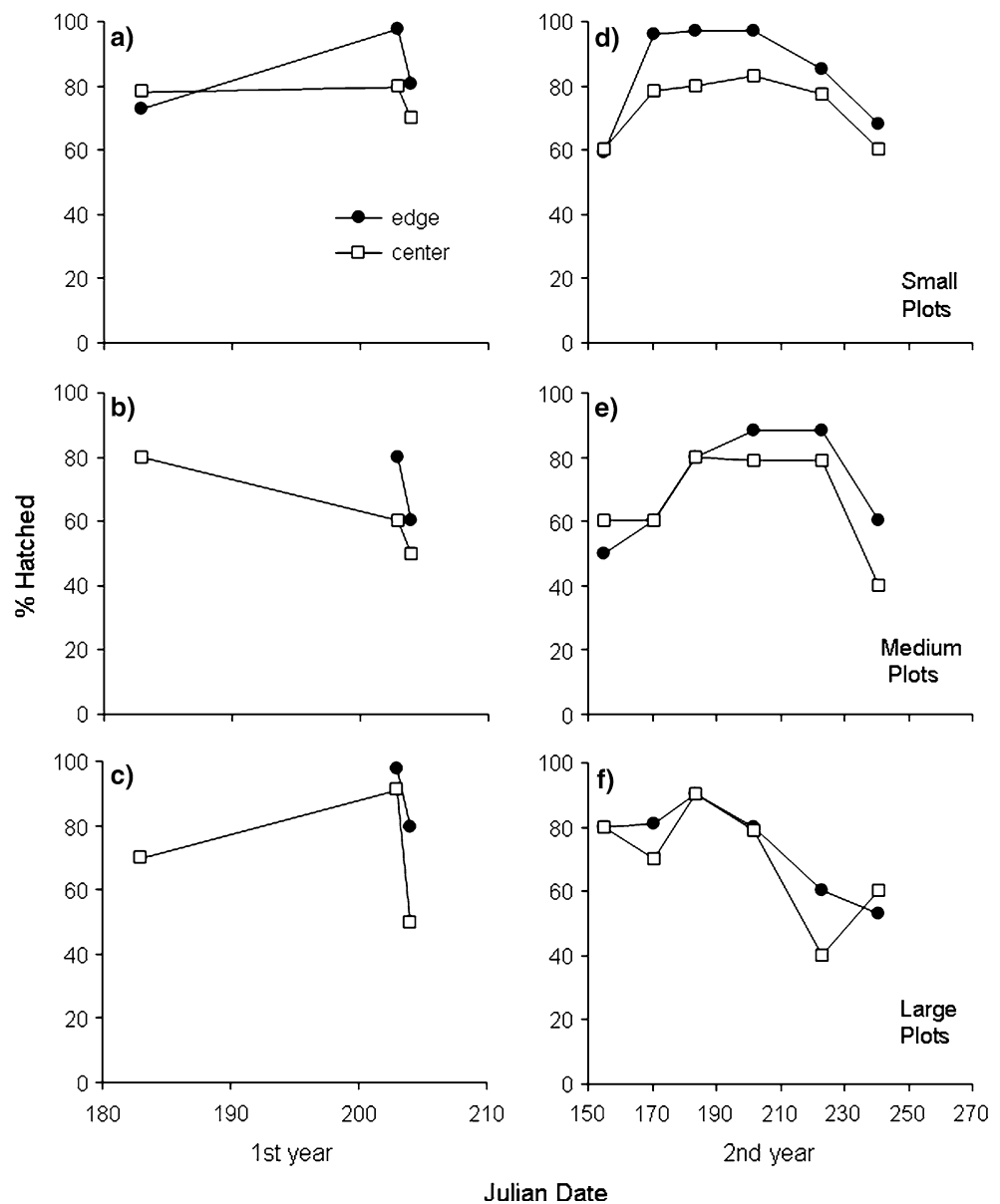
Discussion

The simple, quick, qualitative empirical experiments reported here revealed considerable variability in patch size and edge effects in the insect populations studied (Appendix S3 in [ESM](#)). The natural enemies, *Trichogramma* spp. and adult *C. maculata*, responded to patch size and edges as patch theory and the null-edge hypothesis would predict; their density was higher in the large patches than in the smaller ones, and they had lower densities at edges when next to a poorer patch. Predation rates and

parasitism rates were also higher in larger patches and lower in patch edges than the center. However, both species showed reflecting-type edge effects in small patches. The larger patches may have been of higher quality through a combination of higher colonization, reproduction and survival than the smaller patches. Furthermore, the lack of response to the edge in larger patches for these species suggests that they would probably not be retained in a typical maize field (>20 ha) when they reach the edge.

Particularly intriguing are the higher densities of *O. nubilalis* larvae, and possibly *Chrysopa* spp. eggs, and *R. maidis* at patch edges than patch centers. This “attracting-type” edge effect could arise from higher attraction to the shorter, bushier plants at edges by ovipositing insects, which could have resulted in higher

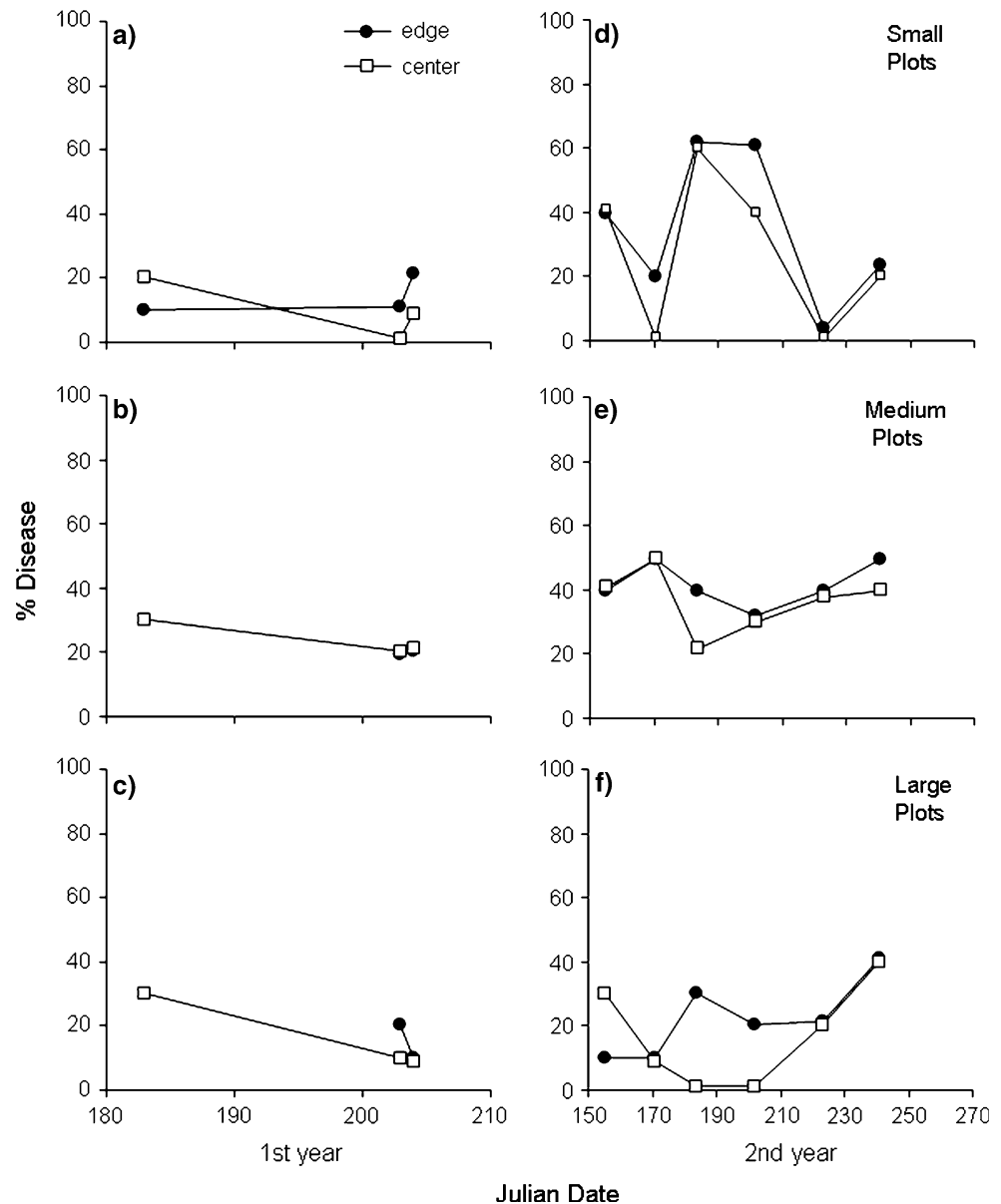
Fig. 4 Percentage hatching (a–f) of *O. nubilalis* egg masses in relation to date, patch size and location within the patch



reproduction. However, *O. nubilalis* egg predation and parasitism was higher and egg hatch was lower in the center than the edges of the large patches, suggesting that predation on eggs – rather than differential oviposition rates – may explain the higher densities of larvae at edges of large patches. Indeed, *C. maculata* is an important predator of both *O. nubilalis* eggs (Andow and Risch 1985) and *R. padi* (Schellhorn and Andow 1999). These results suggest that predators and parasitoids may be an important factor structuring the spatial distribution of two important maize herbivores. Adult *Hippodamia* spp. and immature coccinellid species did not respond to patch size and they showed a reflecting-type patch edge response. *Hippodamia* spp. and the smaller coccinellid immatures are not major *O. nubilalis* egg predators.

Two meters of bare ground around each patch and the surrounding non-maize habitats (bare ground fallow, hedgerows, dirt roads and wheat) were poor reproductive habitats for the species studied. Although the wheat field is a very good habitat for *Hippodamia* spp., and *Chrysopa* spp., and *C. maculata* and European corn borer are found in wheat through May (data from previous studies), the wheat was gone by the second (July 3) of our five sampling dates. The wheat field is not a habitat for *R. maidis*. There tended to be more *C. maculata* and *Hippodamia* spp. adults at the maize edges closest to the wheat field, but we do not believe that the wheat field influenced the interaction between *Trichogramma* spp. and the European corn borer, and *C. maculata* and European corn borer in the maize plots. However, the reflecting type edge response of

Fig. 5 Percentage disease (a–f) of *O. nubilalis* egg masses in relation to date, patch size and location within the patch



Hippodamia spp. adults and the observed uniform density within the patch may also have arisen from a lack of perception of boundaries and rapid movement through zero-fitness regions between patches. In this case, a uniform density within a patch would be a consequence of the insect's perception and movement occurring at a larger scale rather than as a result of behavioral responses to patch boundaries. Sampling species distribution in surrounding patches would be useful in guiding studies of the underlying mechanism(s) for a particular species response to edges.

We found a diversity of patch size and edge responses by the insects of our study (Appendix S3 in [ESM](#)). This suggests a classification of species responses in high-quality patches surrounded by low-quality patches: (1)

species in the patch may follow patch theory-type population dynamics and the null-edge model and will not be retained within the patch when they reach the edge, resulting in some 'spill-over' into the adjacent patch; (2a) species that are uniformly distributed within a patch are predicted to be retained in the patch until hosts or prey are no longer sufficiently present regardless of patch size, presumably because resources were initially sufficient to sustain colonization of the patch, and/or (2b) the species does not recognize the boundary because their scale of perception is different than the scale studied; (3) species that are found in greater numbers at the patch edge should (3a) remain at the patch edge until hosts and prey are no longer sufficiently present, and/or (3b) colonize the patch from the edge and have relatively slow penetration of the

Table 1 Mean numbers of adult *Hippodamia* spp., coccinellid larvae and pupae ($n = 342$ plants per location within small and medium patches, and $n = 114$ plants per location within large patches),*Ostrinia nubilalis* ($n = 100$ plants per location within patch size) and percentage parasitism by *Trichogramma* spp. ($n = 15, 20$ and 38 egg masses per location within small medium and large patches)

| Patch size | Location | Parasitism by <i>Trichogramma</i> (%) | | Coccinellids/plant | | <i>Ostrinia nubilalis</i> /plant |
|------------|----------|---------------------------------------|-----------------|-------------------------|------------------|----------------------------------|
| | | JD 203 (1 day) | JD 204 (3 days) | Adult <i>Hippodamia</i> | Larvae and pupae | Larvae |
| Small | Edge | 1.4a | 21.7a | 0.02a | 0.05a | 2.10c |
| | Center | 1.8a | 30.2b | 0.05a | 0.06a | 1.42b |
| | Combined | 1.6a | 25.9a | 0.04a | 0.06a | 1.76b |
| Medium | Edge | 7.2a | 48.0a | 0.05a | 0.02a | 2.49c |
| | Center | 10.3b | 57.1b | 0.02a | 0.02a | 1.32b |
| | Combined | 8.8b | 52.5b | 0.04a | 0.02a | 1.90a |
| Large | Edge | 15.1a | 37.8a | 0.02a | 0.01a | 2.29c |
| | Center | 27.1b | 53.6b | 0.01a | 0.03a | 1.56b |
| | Combined | 21.1c | 45.7b | 0.02a | 0.02a | 1.92a |

Means within location and patch size and mean patch sizes (=combined) followed by different letters are significantly different at $P < 0.05$

patch interior. Additional studies on individual behavior, movement and demography may be useful for confirming this classification.

Because the spatial and temporal distribution of many insect species is dynamic, and top-down and/or bottom-up forces may interact (Rosenheim 1998; Moon and Stiling 2003), studies of landscape dynamics within and among patches may be facilitated by using reaction diffusion models, a generalization of our simple random walk model. Several existing models examine variable responses to patch edges and may be useful in predicting species-specific responses to landscape pattern. For *C. maculata* and *Trichogramma* spp., a patch-dependent diffusion–reaction model in a spatially heterogeneous environment might provide a reasonable first approximation (Régnière et al. 1983; Shigesada and Kawasaki 1997). For those species that are restricted to a single kind of patch, the diffusion–reaction model of Fagan et al. (1999) may be appropriate. In contrast, for those species that are found more often at the edges of patches, the model of Cantrell and Cosner (1993) may be useful. The combination of patch size theory, simple qualitative empirical studies and our model of differential responses to patch edges allows a rapid determination of edge effects in a given environment and provides some guidance in the determination of the mechanisms of species-specific responses, which could be used in reaction diffusion models to predict species interactions among patches.

Landscapes in contemporary industrial societies are composed of habitat patches (e.g. Forman and Godron 1981) of various sizes and shapes, insects are known to respond to patch size and edges and many agricultural landscapes lack variability at the landscape scale. Therefore, theoretical and experimental analysis of patch size

and edge effects could enable a reconstruction of landscape population properties (sensu Risser 1987) or could be incorporated into a scaling up approach (e.g. Melbourne and Chesson 2005) that relates local dynamics to landscape dynamics.

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